

International Council  
For the Exploration of the Sea

C.M. 1999/Y:16  
Theme Session Y: Cod and Haddock  
Recruitment Processes – Integrating  
Stock and Environmental Effects

## Does spatial match-mismatch of spawning and environmental conditions affect recruitment in Baltic cod?

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### Abstract:

Spawning sites for cod in the central and eastern Baltic Sea (ICES Subdivisions 25-32) are located in several deep basins. Environmental conditions (e. g., oxygen concentrations) for successful egg development in these basins differ within and among years. Spatial distributions of adult cod from research vessel surveys relative to these spawning sites also differ between years. These observations suggest that the spawning stock may sometimes be distributed suboptimally with respect to the environmental conditions that allow successful egg development. We test this hypothesis by comparing reproductive success (recruits/egg production) under assumptions of both environmental homogeneity and heterogeneity at cod spawning sites.

## Introduction:

Environmental conditions that affect survival of cod eggs in the Baltic include the concentration of oxygen and level of salinity at the depths of incubation (Plikshs et al. 1993, Wieland et al. 1994, Nissling et al. 1994). Oxygen concentrations and salinities vary horizontally and vertically (Helcom 1996), and the volume of water that has sufficient oxygen and salinity conditions to allow successful hatching can be quantified (Plikshs et al. 1993, Hinrichsen and Wieland 1996, MacKenzie et al. in press). These volumes vary significantly between the different spawning areas within the stock management area (Plikshs et al. 1993).

These observations suggest that if cod spawn in areas where oxygen conditions are too low at egg incubation depths, reproduction will fail and recruitment will decline. Evidence that recruitment is indeed limited by suitable volumes of water ("reproductive volume"; Plikshs et al. 1993) for cod egg development has been accumulating in recent years (Plikshs et al. 1993, Sparholt 1996, Jarre-Teichman et al. in press, Köster et al. 1999), and has contributed to the development of medium-long term management strategies (e.g., determination of biological reference points) for this stock (ICES 1998a; Kuikka et al. 1999).

Most of this evidence has focussed on the temporal variability in total reproductive volume (i. e., inter- and intra-annual variations) and has not considered its spatial variability. Cod in the Baltic spawn in 4 major deep basins (Bornholm, Gdansk, and southern and central Gotland) which correspond approximately to the main ICES subdivisions. The spatial distribution of cod among these basins varies between years (ICES 1998b), as does the spatial distribution of the total reproductive volume within the Baltic Proper (Plikshs et al. 1993). However, most of the modelling efforts which have addressed how reproductive volume affects recruitment have assumed that spatial distributions of both variables are constant over time. In other words, the spatial correspondance between spawning activity and suitable environmental conditions (as represented by reproductive volumes) has been assumed to be similar (or random) in all years.

Given the historical spatial variability in both cod distributions and reproductive volumes, this assumption may be inappropriate. We hypothesize that allowing for the difference in spatial covariation between spawning and the environment might give better estimates of reproductive success than using either total reproductive volume or assuming that the spatial correspondance between spawning and environmental conditions is similar between years.

## Methods:

### Data sources:

#### 1. Cod spatial distributions.

The spatial distribution of the stock has been estimated from the abundance of older fish collected during International Bottom Trawl Surveys used to assess yearclass strength and to tune VPA estimates of population abundance (Sparholt and Tomkiewicz 1998; ICES 1999). These surveys are conducted in February-April and cover the main distributional area of the stock. These data provide age-specific estimates of cod abundance (no. per hour trawling) for the years 1982-present.

#### 2. Cod recruitment.

Recruitment (age 2) estimates are derived from VPA (ICES 1999). The time series used in our analyses was 1982-1994. Years prior to 1982 have not been used because the spatial distribution of the stock is not known. The most recent yearclasses (1995 and 1996) in the available VPA recruitment time series have been excluded from analyses because recent VPA estimates are more uncertain than those farther back in time.

It is presently not possible to identify from which spawning area or subdivision the recruits were produced. As a result recruitment estimates cannot be spatially disaggregated to site of origin.

### 3. Cod survival.

In many fish stocks recruitment depends significantly on a measure of population egg production (Myers and Barrowman 1996, Marteinsdottir and Thorarinsson 1998, Marshall et al. 1998). Such is the case also for cod in the Baltic (Plikshs et al. 1993, Sparholt 1996, Jarre-Teichman et al. in press; ICES 1999; Fig. 1). As a result we compared time series of recruitment adjusted for interannual differences in egg production with reproductive volume data.

The correction for egg production was done by calculating survival estimates during the first 2 years of life:

$$\% S = R/E$$

where R is age 2 recruits from VPA and E is annual population egg production.

Egg production was estimated from the numbers and combined-sex weights of fish in the stock (ICES 1999) combined with reproductive biology information. Age-specific sex ratios and female maturity ogives applied in the estimates were those compiled from research surveys by Tomkiewicz et al. (1997) and used in working group assessments (e. g., ICES 1998b, 1999). These inputs are available spatially resolved on a subdivision basis and are averaged for various time intervals (typically 5 years) during the time series.

Individual relative fecundity estimates (no. eggs per gram female body weight) for eastern Baltic cod have been measured by Kraus et al. (submitted) for the years 1987-1992, 1995, 1996, and Bleil and Oeberst (1996) for 1994 and 1995. These data have been used in our egg production calculations. For the years 1982-1986, we assumed that an average (weighted for sample size) of Kraus et al.'s data for 1987-1989 was representative; for 1993, we assumed that a weighted average of Kraus et al.'s data for 1992 and Bleil and Oeberst's data for 1994 (Subdivision 25) was representative. Relative fecundity estimates in Baltic cod show insignificant variation between months within a year and between subdivisions within a month, and are independent of body size (Kraus et al. submitted). We assumed that relative fecundity estimates in one subdivision therefore represented mean annual fecundities throughout the assessment area.

The egg production in each spawning area was estimated according to the age-specific spatial distribution of cod as determined by research surveys. For these purposes we assumed that cod in each subdivision spawned in its main deep basin (Table 1):

The relative distribution of cod among the three main subdivision allowed us to calculate the fractions of egg production in each subdivision. In the case of Subdivision 26, which had two spawning areas (i.e. the Gdansk Deep and the southern Gotland Basin), we re-analysed the original trawl survey data according to haul location to determine which trawls were located in each of the spawning areas. This allowed us to sub-fractionate cod abundances within this subdivision to each of the two spawning areas.

#### 4. Reproductive volumes.

Reproductive volumes for each basin have been calculated (Plikshs et al. 1993), intercalibrated (MacKenzie et al. in press) with independent data (Hinrichsen and Wieland 1996) and adjusted (Jarre-Teichman et al. in press) to account for seasonal differences in reproductive volume (MacKenzie et al. 1996a, b) and for interannual differences in peak spawning time (Wieland et al. in press). The reproductive volume time series used by Jarre-Teichman et al. (in press) has been updated for observations in recent years (Plikshs, unpub. data). The adjustment for variations in peak spawning time was accomplished by calculating average reproductive volumes over the months that correspond to the main spawning period in each year (see details in Jarre-Teichman et al. in press). This calculation assumes that spawning time in all four basins is similar and described by spawning time estimates for the Bornholm Basin (Wieland et al. in press); violations of this assumption may require different averaging periods for different spawning areas (e. g., Plikshs et al. 1999) to be used in future analyses.

#### 5. General statistical approach:

Our null hypothesis was that survival varied independently of the spatial overlap of egg production and reproductive volume distributions. Data analyses were done in two-steps: first, annual survival was compared with total reproductive volume in the eastern Baltic estimated at spawning time, as given by the sum of volumes in the Bornholm, Gdansk and southern and central Gotland Basins. This comparison assumes spatial homogeneity of both egg production and reproductive volume but allows for interannual variability in both variables.

Second, an index of spatial overlap of the egg production and reproductive volume spatial distributions was developed and compared with the survival rate. These comparisons allow for the possibility that egg production and reproductive volume distributions may not coincide. The index of spatial overlap was derived from the product of the proportions of total egg production and total reproductive volume that occurred in each spawning area. These products were calculated for each spawning area and then summed to give an index of overlap for each year. The overlap index used is the coefficient of overlap,  $C_\lambda$  (Horn 1966):

$$C_\lambda = 2 * \sum((RV_i/RV_{total}) * (EP_i/EP_{total})) / (\sum(RV_i/RV_{total})^2 + \sum(EP_i/EP_{total})^2)$$

where RV = reproductive volume, EP = egg production, and the summations are over the  $i = 4$  spawning areas. This index ranges from 0 to 1 corresponding to dissimilar to completely overlapping distributions.  $C_\lambda$  was then used in scatterplots and linear regression analyses to test the hypothesis that survival was independent of the overlap between egg production and reproductive volume distributions.

#### Results:

##### *Spatial and temporal distribution of egg production and reproductive volume:*

The contribution of each of the main spawning areas to total egg production has varied during the time period (Fig. 2, 4). In some areas, relative proportions have decreased or increased over the

entire time series. Total egg production in the eastern Baltic has decreased substantially since the early 1980's and increased again slightly in the recent years.

The relative contribution of each area to the total reproductive volume has also varied during the same period (Fig. 4). Volumes in particular basins only partly covary with variations in other basins (Table 2).

Total reproductive volumes in the period considered here (1982-1994) show much less short-term variability than in previous years (Fig. 5). Prior to 1982, reproductive volumes frequently were high ( $> 300 \text{ km}^3$ ) and low-volume periods (e. g., years with volumes  $< 200 \text{ km}^3$ ) lasted only one year (Fig. 5). Total volumes at spawning time during 1966-1981 and 1982-1994 were respectively  $300 \pm 173 \text{ (SD)}$  and  $167 \pm 105 \text{ km}^3$ .

#### *Effects of spatial and temporal variability in reproductive volume and egg production on survival:*

The index of spatial overlap of egg production and reproductive volume has fluctuated during the years 1982-1994 with an overall increase (Fig. 6). Survival between the egg stage and recruitment at age 2 averaged 0.00018% (st. dev. = 0.0001) during 1982-1994 and was higher in the early 1990's than in other years (Fig. 6).

Survival was always low when total reproductive volume was low (i. e.,  $< \text{ca. } 120 \text{ km}^3$ ; 6 years out of 6) but was sometimes high (3 years out of 7) when reproductive volumes were higher (Fig. 7). As a result the relationship between survival and total reproductive volume cannot be described with simple regression models (Fig. 7). However when survival estimates were compared with the overlap indices, they tended to be higher when egg production and reproductive volume distributions were similar (Fig. 8). This relationship becomes stronger if one outlier year (1991) is excluded from the calculations (Table 3).

#### Discussion:

Previous studies using longer time series have shown that recruitment in Baltic cod varies with both egg production and reproductive volume (Plikshs et al. 1993, Sparholt 1996, Jarre-Teichman et al. in press, Koster et al. 1999). In this study we have also found that egg production and reproductive volume at spawning time affects survival and recruitment. Our results are strongest when one large outlier year is excluded from the analysis. Reasons for the anomalously high survival despite low overlap and low reproductive volume in this year are unclear, but could perhaps be associated with various sampling errors (e. g., survey spatial distributions, recruit estimates, egg production estimates) and should be investigated in future.

Our results regarding relative spatial distributions of egg production and reproductive volume for the remaining yearclasses 1982-1994 differ from previous findings because they show that (1) differences in the spatial overlap of egg production and reproductive volume can affect survival to recruitment and (2) survival is always low when total reproductive volume is low.

These results suggest two scenarios by which the environment will affect survival rates in this stock (Table 3). In one scenario a high reproductive volume does not limit egg survival (specifically, egg hatch success) in any of the spawning areas, and the spatial distribution of egg production relative to this factor is unimportant for ensuring high survival. In this case, survival can potentially, although not necessarily, be high and recruitment will be limited by other processes (e. g., egg predation by clupeids; Köster and Schnack 1994; Sparholt 1996).

In the other scenario, low reproductive volumes limit egg survival in some or all spawning areas. In this case, a prerequisite for high survival will be a distribution of eggs that matches the distribution of reproductive volumes. Without high overlap between these distributions in low reproductive volume years, survival will probably be low. If there is high overlap in such years, survival (egg hatch success) can potentially still be low due to limiting reproductive volume. For example recent studies show that egg buoyancy in Baltic cod depends on female size and batch number (Nissling et al. 1994; Vallin and Nissling submitted). A population structure producing a higher share of negatively buoyant eggs in relatively low reproductive volume years even when there is a high spatial overlap of egg production and reproductive volume will still not likely produce a strong yearclass. Furthermore, even given a horizontal match of egg production and high reproductive volume, the eggs may develop in an intermediate water layer with sufficient salinity but insufficient oxygen concentration. These hydrographic situations have been observed in the Bornholm Basin in 1986 (Wieland 1988) as well as in the Gotland Basin in 1994 (Plikshs et al. 1999).

We interpret these results as preliminary evidence that a match-mismatch relationship between egg production and reproductive volume may be an important prerequisite for successful recruitment and survival in Baltic cod via the influence of oxygen and salinity on egg hatch success. In this case, the match-mismatch relationship involves egg production distributions and the abiotic environment to which they are exposed, rather than the more familiar match-mismatch relationship between larval feeding success after yolk sac absorption and prey availability (Cushing 1982). Nevertheless, the underlying concept is the same: a favorable correspondence between an early life history stage and an environmental feature is a necessary prerequisite for improved survival.

The ecological explanation for these results is probably associated with the fact that eggs produced in areas with low oxygen conditions will have a low chance of hatching (Wieland et al. 1994). As a result eggs produced in such areas are essentially lost and the "effective" egg production (expressed in terms of the production of larvae and recruited fish) in such areas will be extremely low. For example, during 1982-1983, approximately 80% of the egg production was located in the two Gotland and Gdansk Basin spawning areas. However during these years, estimated reproductive volumes for all three areas were close to zero (Fig. 3), indicating that most of the egg production in these years had essentially no chance of survival. Given this spatial mismatch between egg production and reproductive volume, it is perhaps not surprising that recruitment (numbers of 2 year olds from MSVPA) declined substantially (ca. 50%) during each of these years despite record high levels of spawning stock biomass (ICES 1997a).

Our results assume that the spatial distribution of adult fish at spawning time is adequately described by the IBTS surveys. While it is generally accepted that the surveys do indicate the relative abundance of adults (ICES 1999), it is not clear whether the spatial distribution at spawning time is similar to that at the time of the survey. In the early years of our time series this may have been the case because spawning time was earlier in the year (1-2 months after the survey) during the early-mid 1980's than during the last 5-10 years when it has shifted to summer months (Jarre-Teichman et al in press; Wieland et al. in press). As a result spatial distributions of egg production in the recent years may be less certain than earlier. Alternative estimates of adult spatial distribution at spawning time would be desirable for comparison with those used here. These could perhaps be derived from analysis of catch-effort data, VPA-type analyses for specific subdivisions (Köster et al. 1999) or from ichthyoplankton data in spawning areas.

Inspection of the time trend in survival showed that survival was generally higher in the early 1990's than in other years. Factors other than reproductive volume – egg production relationships have also undergone major changes during the same time period and these might have increased cod survival. For example, cannibalism as estimated by MSVPA has decreased during

the period 1982-1995 (ICES 1997a; Neuenfeldt and Köster in press). Since most of the cannibalism involves mortality of 0- and 1-group cod (Sparholt 1994), it is possible that lower cannibalism of pre-recruits may have been associated with the increase in survival.

A second reason for the higher survival in the early 1990's could be due to underestimation of the spawning stock and egg production. During some of these years (e. g., 1992 and 1993), unreported landings were a substantial proportion (i.e., 1992 and 1993: 82% and 153%) of the official landings (ICES 1997b, 1998c). When corrected for unreported landings, estimated spawning stock sizes for these 2 years were therefore 68 and 43% higher than those calculated using official landings (ICES 1997b). These estimates suggest that the true spawning stock (and egg production) may have been higher during these years. As a result unreported landings could have contributed to the apparently higher survival rates in 1992 and 1993 that we have derived from VPA based on official landings (ICES 1999). However, the increase in survival in 1992-1993 when compared with 1987-1990 is 2-3 fold (Fig. 6), which greatly exceeds the increase in survival that can be explained by the estimated incidence of unreported landings.

The survival rates calculated here should not be interpreted directly as early life history survival rates because they cover a time period (2 years) extending much beyond the early life history phase which might last only up to 4-6 months if egg, larval, and pelagic 0-group stage are considered. Our survival rates were constructed only to demonstrate the relevance of reproductive volumes as an important habitat characteristic and probably underestimate survival during the early life history (i. e., pelagic) phase. Survival during this phase, which might be more closely related to reproductive volume variations than that indicated in our analyses, could not be estimated because reliable abundance estimates for some developmental stages (e. g., pelagic 0-groups) do not presently exist. Moreover the survival rates themselves are approximations which involve numerous assumptions (e.g., consistent sampling methods and catchability on research surveys in all years, sensitivity of egg production estimates to variations in adult reproductive biology [Marshall et al. 1998, MacKenzie et al. 1998]). Some of the residual variation in our analyses may be due to violation of these assumptions, as well as inaccuracies in the reproductive volume determinations themselves.

Our results suggest that higher resolution of (1) the spatial distribution of those environmental characteristics which increase survival probability and (2) the spatial distribution of egg production are both necessary to estimate the influence of total population egg production on the abundance of subsequent stages (e. g. recruits) in Baltic cod. New egg production models, which accomodate spatial (and temporal) *heterogeneity* in egg production and survival, might yield better estimates of recruitment than those which assume spatial and temporal *homogeneity* of egg production and survival among spawning areas (times) within a given stock.

Table 1. Spawning areas in each of the main ICES subdivisions of the eastern Baltic.

ICES Subdivision	Spawning Area
25	Bornholm Basin
26	Gdansk Basin
26	Southern Gotland Basin
28	Central Gotland Basin

Table 2. Matrix of correlation coefficients (Pearson  $r$ ; top) and probability values (bottom) for 13 years (1982-1994) of reproductive volume data in 4 spawning basins for cod in the eastern Baltic Sea.

	Gdansk	South. Gotland	Cen. Gotland
Bornholm	0.76 0.0023	0.31 0.29	0.44 0.13
Gdansk		0.53 0.0598	0.65 0.0169
South. Gotland			0.49 0.0908



Table 3. Statistical summary of regression analyses of factors influencing survival of cod eggs to age of recruitment (2 years) in the eastern Baltic Sea (ICES Subdivisions 25-32). Note that % S is the percent survival of eggs to the recruitment age (2 years),  $RV_{total}$  is the total reproductive volume at spawning time, Overlap ( $C_{\lambda}$ ; Horn 1966) is an index of overlap between relative spatial distributions of egg production and reproductive volume, and P is the statistical significance level for the overall regression model. See Methods for computational details and data sources.

Model	Yearclasses	$R^2$	P
% S = $0.0002 \times \text{Overlap}$ + $7 \times 10^{-5}$	1982-1994	15%	$0.10 < P < 0.20$
% S = $1.0 \times 10^{-7} \times RV_{total}$ + $2 \times 10^{-4}$	1982-1994	2%	$> 0.20$
% S = $3 \times 10^{-4} \times \text{Overlap}$ + $2 \times 10^{-5}$	1982-1994; excl. 1991	37%	$0.02 < P < 0.05$
% S = $1.0 \times 10^{-7} \times RV_{total}$ + $1 \times 10^{-4}$	1982-1994; excl. 1991	2%	$> 0.20$

Table 4. Schematic summary of interactions between total reproductive volume and the spatial overlap of egg production and reproductive volume distributions on hatch success of cod eggs in the eastern Baltic Sea.

	Low Reproductive Volume	High Reproductive Volume
Low Overlap	Low hatch success	High hatch success
High Overlap	?? (depends on egg buoyancy)	High hatch success

# Figure captions:

Figure 1. The influence of total egg production on recruitment (age 2 from VPA) for cod in the eastern Baltic Sea (ICES subdivisions 25-32).

Figure 2. Estimated annual production of cod eggs in different spawning areas of the eastern Baltic Sea for the years 1982-1994.

Figure 3. Reproductive volumes at spawning time in different spawning areas of the eastern Baltic Sea for the years 1982-1994.

Figure 4. Proportions of total egg production and reproductive volume in the Baltic Sea in each of four spawning areas for the years 1982-1994. Circles: egg production. Squares: reproductive volume.

Figure 5. Interannual variability in reproductive volume at spawning time during the years 1966-1994. Two periods having different levels of reproductive volume are shown.

Figure 6. Interannual variability in survival from the egg stage to age 2 (see text for calculation) for cod in the eastern Baltic Sea, total reproductive volume ( $\text{km}^3$ ), and overlap ( $C_\lambda$ ) between relative spatial distributions of egg production and reproductive volume.

Figure 7. Interannual variability in survival from egg to age 2 compared to total reproductive volume in the eastern Baltic Sea. Note the low survival rates at low reproductive volumes.

Figure 8. Interannual variability in survival from egg to age 2 compared to the spatial overlap of relative distributions of egg production and reproductive volume in four spawning areas in the eastern Baltic Sea. See also Table 2 for regression statistics.

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*Recruitment is higher when egg production is higher...*

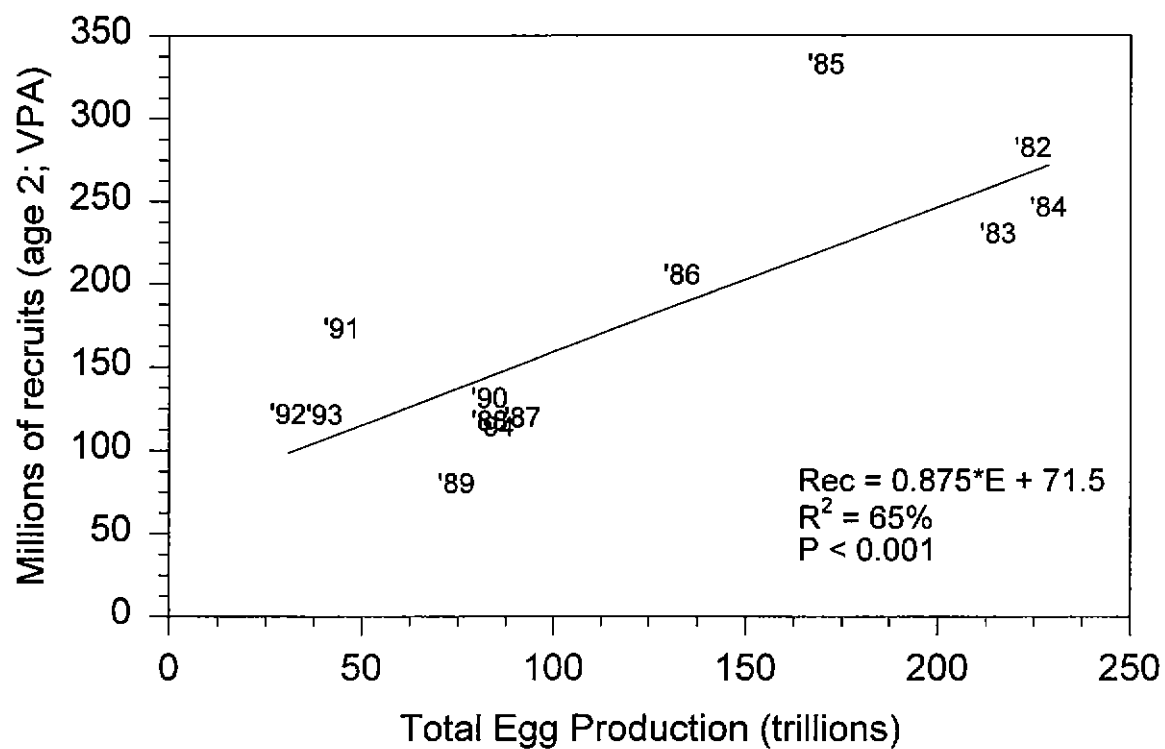


Figure 1

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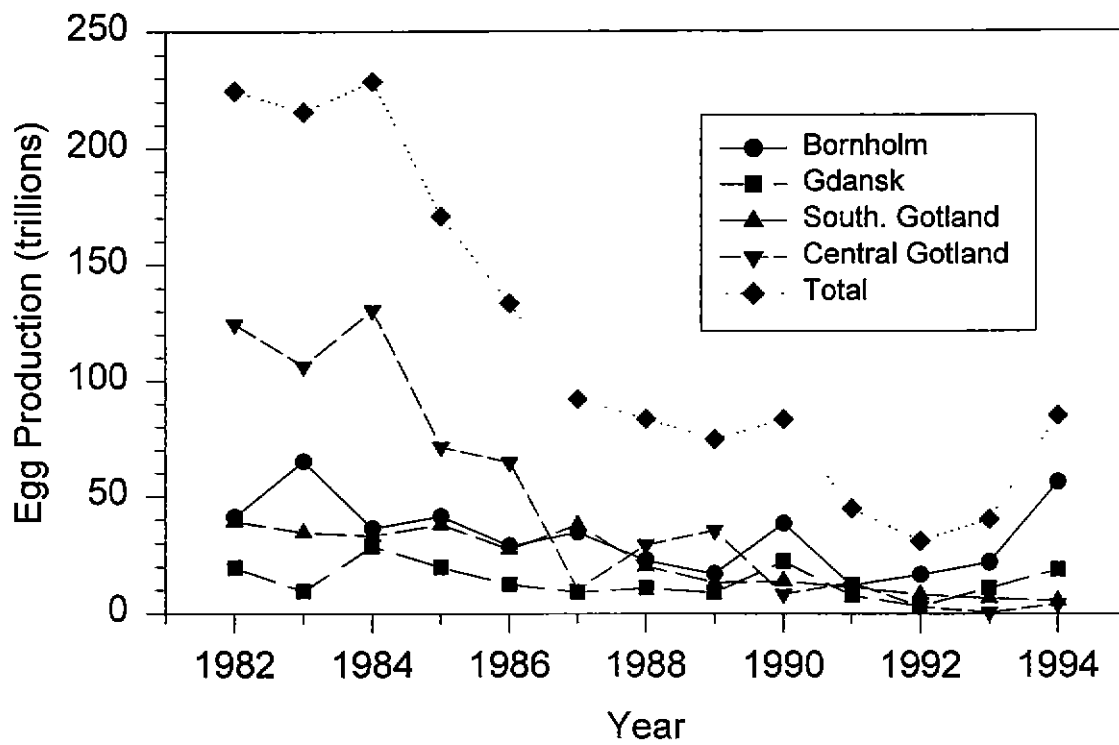


Figure 2

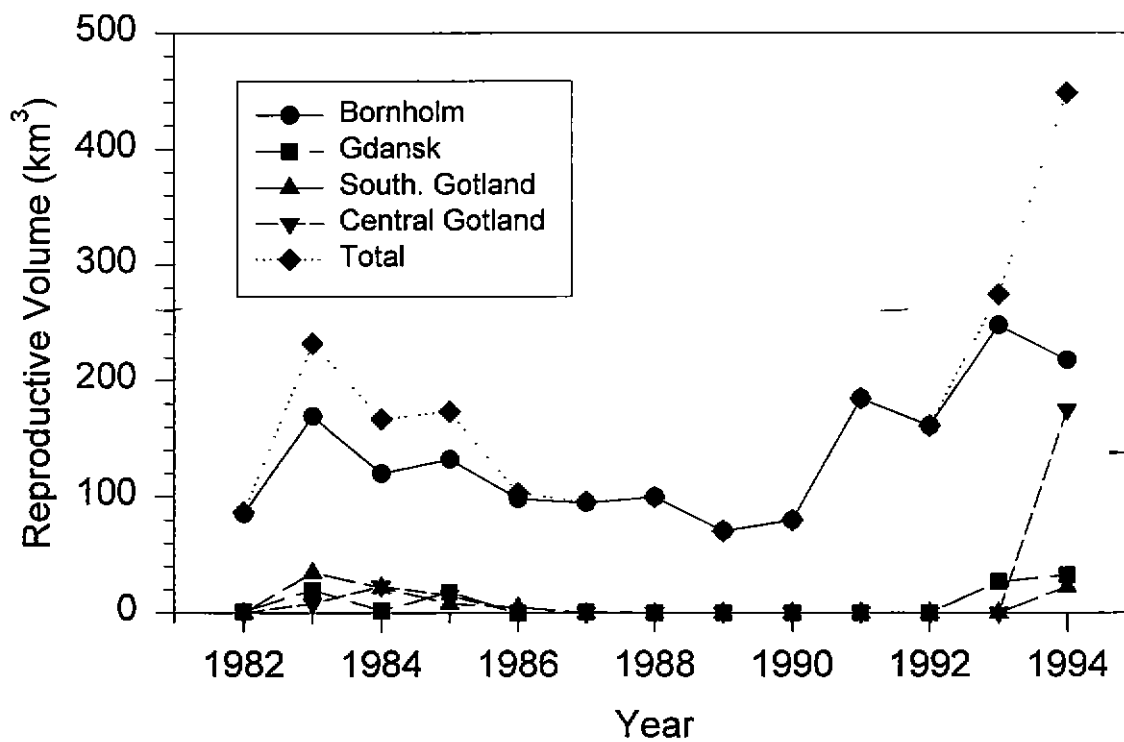


Figure 3

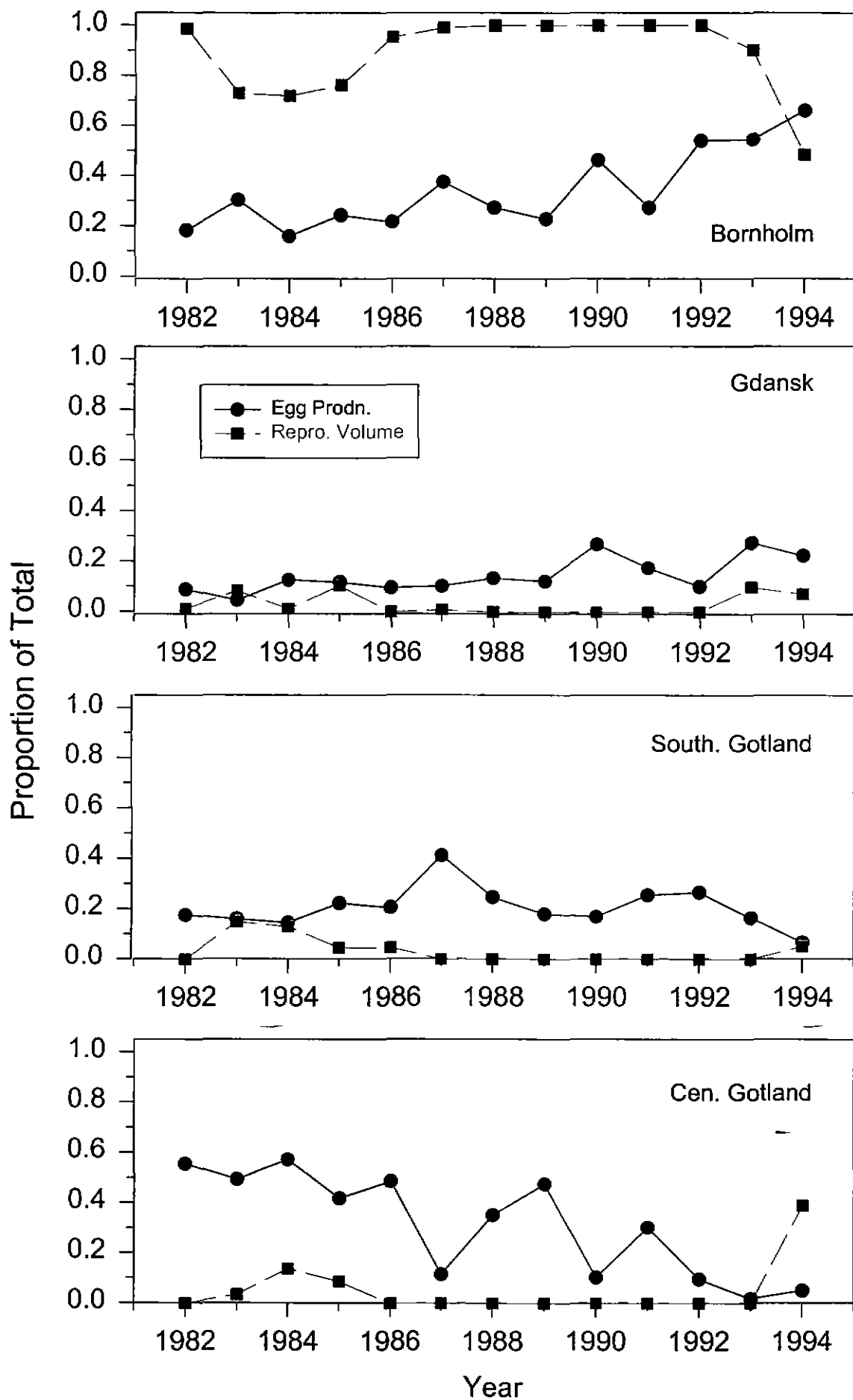


Figure 4

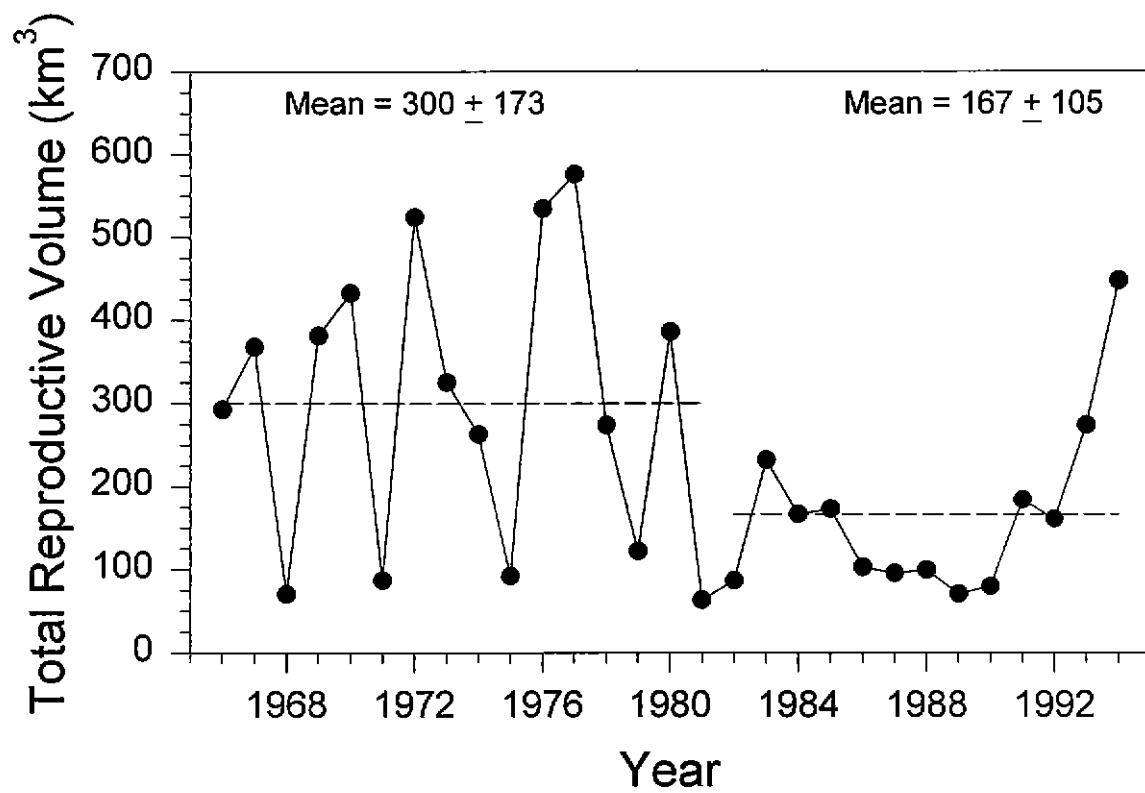


Figure 5 \_

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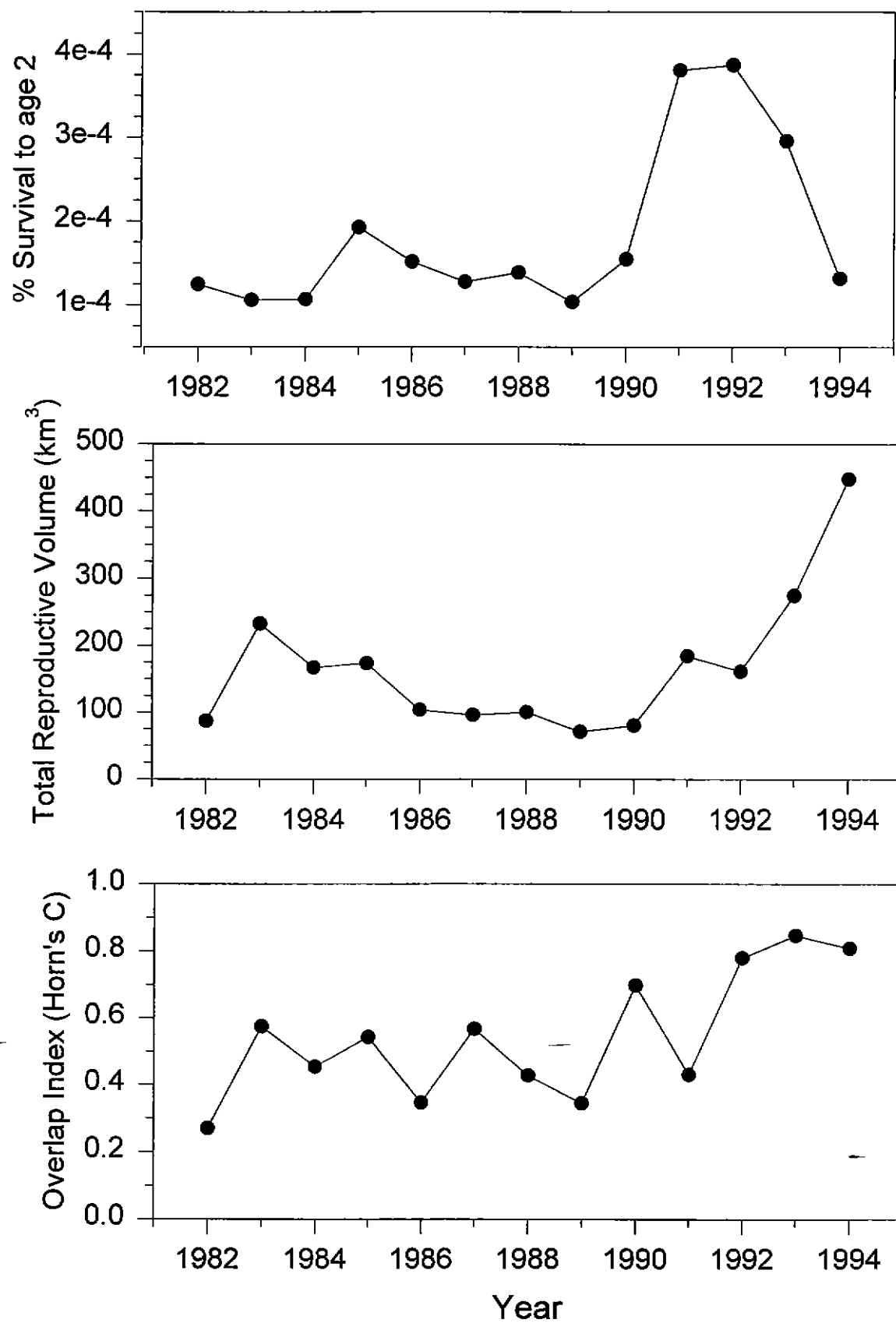


Figure 6

h:\brm\match\match5.jnb

*Low Survival Probability if Reproductive Volume is Low...*

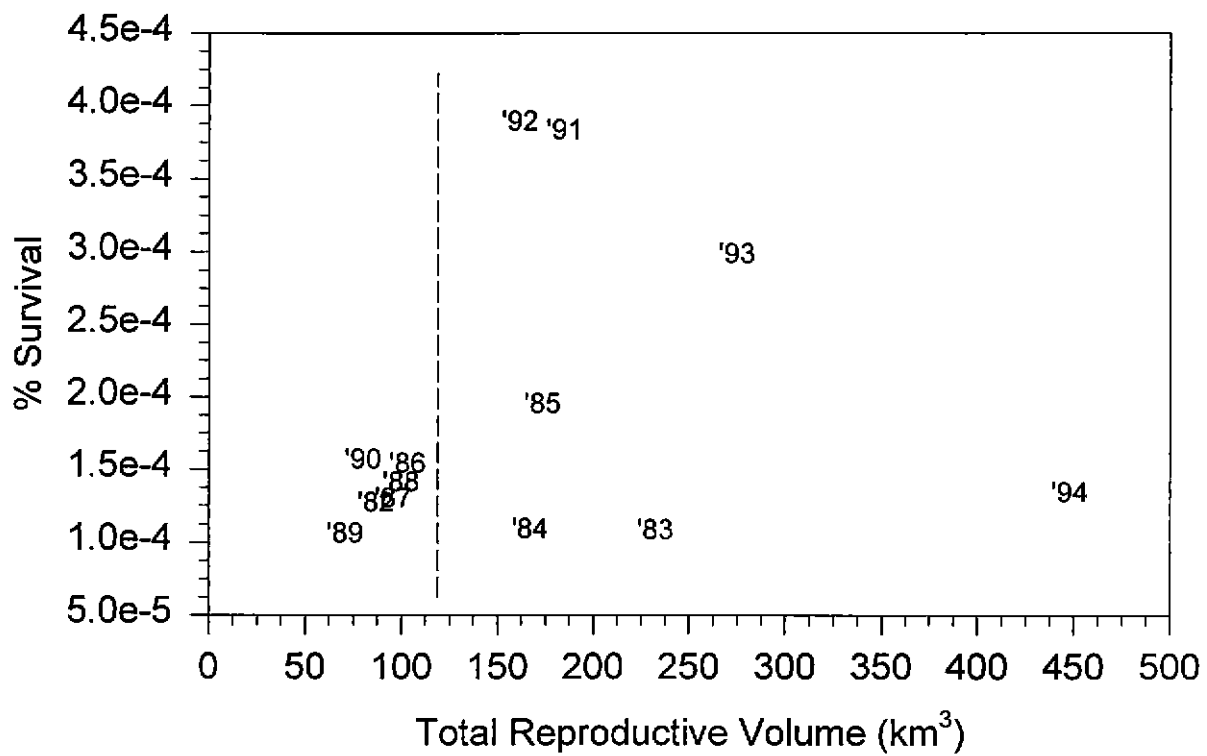


Figure 7

*Higher Survival Probability if Higher Spatial Overlap...*

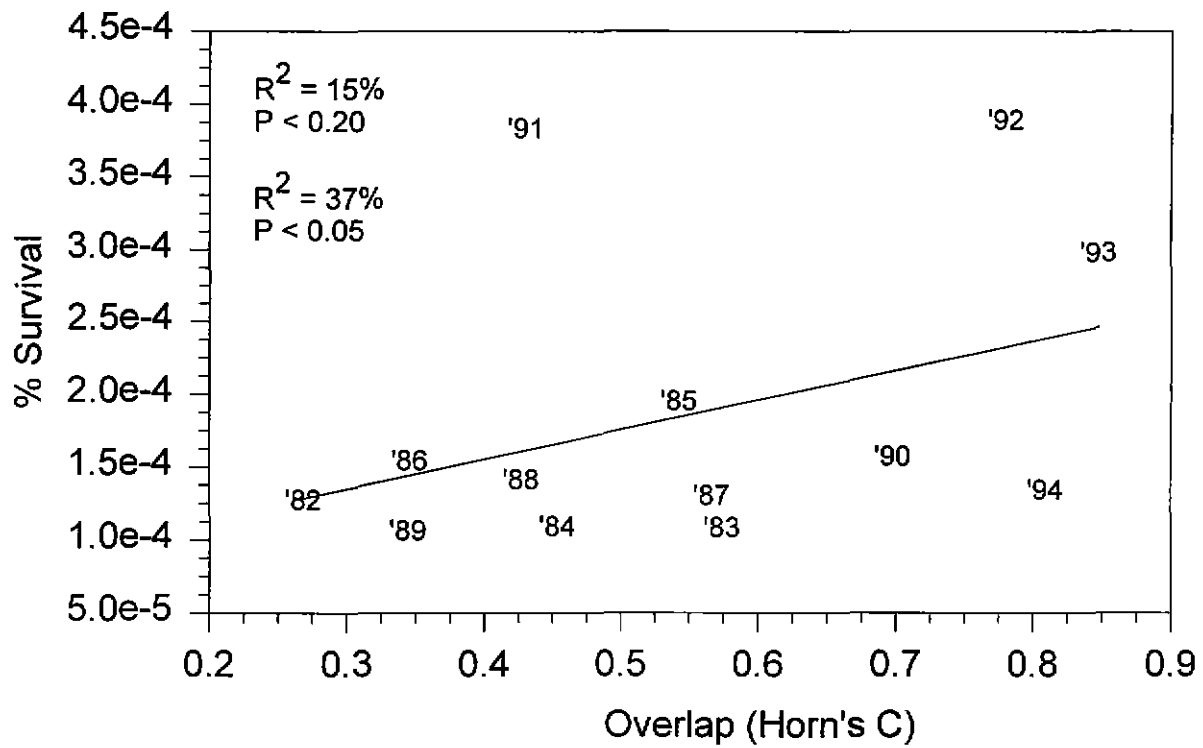


Figure 8

h\brm\match\match7.jnb